A database approach to studies of molluscan taxonomy, biogeography and diversity, with examples from western Atlantic marine gastropods

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Abstract: A system of data fields and conventions is introduced that will allow workers on any group of mollusks to build interactive databases documenting classifications, synonymies, geographic and bathymetric ranges, and other summary information at the species level. This system is used to build a database which is the first comprehensive catalogue of Recent Western Atlantic gastropods ever assembled with geographic coverage extending from Greenland to Antarctica. As of January 1993, the database contained 8370 records, of which 3988 represent currently recognized species, 3491 are synonyms, 157 are *nomina dubia* and the remainder are misidentifications, misspellings, invalidly published or extralimital.

There are 3103 currently recognized species of tropical Western Atlantic gastropods (35°N to 24°S); 2641 of these had been named by 1971, when Keen documented 2438 gastropod species in the tropical Eastern Pacific. The common perception that the tropical Western Atlantic fauna is depauperate compared to the Eastern Pacific cannot be supported.

Faunal lists corrected for synonymies, variant generic combinations and misidentifications were extracted from the database for eight areas in the tropical Western Atlantic. These are eastern and western Florida, Yucatan, Panama, Jamaica, Puerto Rico, the Netherlands Antilles and northern Brazil. To correct for regional collecting biases, species smaller than 5 mm, those occurring only deeper than 50 meters, and those lacking external shells were excluded from the lists. In 28 pairwise comparisons among the standardized lists, 27 showed faunal similarities greater than 50%. Western Florida, which lacks shallow reefal habitats, had faunal similarities lower than did eastern Florida, which has these habitats. Habitat availability seems as important as geographic distance in determining faunal similarity within the tropical Western Atlantic. None of the eight regions had more than 4% endemic species. Although species tend to be widespread within the tropical Western Atlantic, only 20% are known from other biogeographic provinces.

Studies of mollusks in the Western Atlantic and throughout the world are hindered by the lack of up-to-date systematic and faunal lists. Researchers attempting to identify or describe species have no comprehensive list of candidate species for comparison. Different names are used for the same species in different regions, making faunal comparisons difficult. Researchers trying to document the effects of extinction, immigration, and speciation on the diversity of various faunas find that reliable estimates of levels of diversity are impossible to obtain even for most shallow-water faunas. Several published catalogues have covered parts of the Western Atlantic fauna in the Northern Hemisphere (Dall, 1889b; Maury, 1922; Johnson, 1934; Abbott, 1974; Turgeon *et al.*, 1988). No catalogue has ever been assembled for the entire Western Atlantic, nor for the tropical Western Atlantic biogeographic province.

Even in such intensively studied areas as the Mediterranean, malacological research has suffered from the lack of comprehensive lists of taxa. Sabelli *et al.* (1990) note the salutary effects of the first modern catalogue of Mediterranean shell-bearing mollusks, that of Piani (1980): a) many researchers adopted the proposed classification thus stabilizing nomenclature; b) the Italian Malacological Society began censusing the Italian marine mollusks, "which would have been inconceivable without a reliable reference list"; c) other researchers were stimulated to produce similar catalogues of Mediterranean opisthobranchs, aplacophorans and cephalopods. Sabelli *et al.* (1990, 1992) themselves recently have finished a 781 page annotated catalogue of Mediterranean mollusks.

The electronic database represents the next step in the production of such catalogues. The potential value of databases in biological research is well-known (Allkin and Bisby, 1984), but this potential has not been realized in malacology. The structure of data fields and conventions introduced here will allow workers on any group of mollusks to build interactive databases documenting classifications, synonymies, geographic and depth ranges, etc. Printed catalogues are static, whereas databases are dynamic. Information in a database can be reorganized (alphabetically, systematically, geographically, chronologically, etc.) to suit the needs of the user. It can be queried in numerous ways, limited only by the ingenuity of the researcher and the types of raw data utilized by the database.

A database must be designed to maximize its ability to answer the questions most likely to be asked of it. A single database that could address the needs of all fields of molluscan research would be extremely complex and cum-

bersome. The species-level database discussed here has a coarser level of focus than a collection database, summarizing information about the species overall, rather than about particular samples (lots) of a species. Coverage includes all Recent marine gastropod species reported in the Western Atlantic from Greenland to Antarctica.

MATERIALS AND METHODS

More than 1,000 publications on Western Atlantic gastropods were scanned for taxonomic, and bathymetric information. These publications are listed in a bibliographic database linked to the species database. Data come primarily from the published literature, but have also been taken from the malacological collections at the Academy of Natural Sciences of Philadelphia (ANSP) and solicited from researchers expert on the systematics of particular groups. The database contains references to sources of information about each species, to allow verification of the data.

For each species-level name applied to a Western Atlantic gastropod, the database attempts to document its status as available, valid, synonymous, dubious, misidentified or misspelled. Note that a species can be valid (i.e. currently recognized), while its currently used name is invalid (e.g. preoccupied). Table 1 lists the fields of information tracked, and the space allocated to them; these fields are described below. Information about geographic, depth and size ranges is entered under the specific name used in a given publication. Geographic, depth, and size data are combined over synonyms to generate summary data for each currently recognized species. If the status of a name is changed from synonymous to valid, or moved from the synonymy of one species to another, its data move with it. The database is thus self-correcting to the degree that the literature provides corrections. Figure 1 shows a subset of database fields and their contents.

The database is currently implemented in Paradox 4.0, but can be easily transported in database or delimited ASCII format to other database programs. It can also be linked to collection databases for comparison of range data and synonymies. The database currently occupies 17 megabytes as a database file, or about 2 megabytes as a delimited ASCII file. A 386 computer or the equivalent is needed for satisfactory performance. [Subsets of the database are available electronically, via Internet from Rosenberg@say.acnatsci.edu.]

TABLE 1. Data fields used in the database. Numbers give character length of field; N = numeric, A = alphanumeric.

Systematic number	N
Family	A25
Genus	A20
Subgenus	A20
Species	A20
Subspecies	A20
Associated name	A20
Status 1	A1
Status 2	A3
Author	A40
Date	N
Abc	A1
Attributed author	A40
Original genus	A20
Parentheses	A1
Combining genera	A60
Combination	A60
Citation	A20
Figure	A50
Other figure	A50
Type locality	A120
All localities	A150
Ocean	A15
Shell	A1
North	N
South	N
East	N
West	N
Shallow	N
Deep	N
Live shallow	N
Live deep	N
Size	N
Comments	A150
References	A150

DATABASE STRUCTURE AND FORMAT

Data fields, data types and character limits are listed in Table 1; conventions for data entry are described here. Examples of the contents of some fields are shown in Figure 1.

SYSTEMATIC NUMBER: Each family is assigned a number, to allow sorting in systematic order. Alternate classifications can be accommodated by adding fields for numbering schemes that would allow sorting in different orders.

FAMILY: Family names and classification follow Ponder and Warén (1988), Rosenberg (1992) and other recent works.

GENUS: Generic classification follows Turgeon *et al.* (1988), Vaught (1989), and other recent works. Authorities for generic placements are cited in **references.**

SUBGENUS: Conventions are the same as for **genus**. Few data pertaining to subgenera have been entered because

there is little agreement on subgeneric classifications and many authors of systematic works do not provide subgeneric placements for the species they treat.

SPECIES: Only the valid or currently recognized specific name of a species is entered here; synonymous names are entered under **associated name**. In cases where species previously synonymized have been recognized as valid by recent workers, citations are given in **references**.

SUBSPECIES: Only the valid or currently recognized subspecific name of a subspecies is entered here; synonymous names are entered under **associated name**. Most subspecies reported in the malacological literature occur sympatrically with the nominate subspecies, because malacological workers until recently treated forms and varieties as subspecies. Subspecies are therefore considered to be synonyms of the nominate form, except in cases where authors have presented evidence for geographical separation of ranges or have raised subspecies to full species.

ASSOCIATED NAME: This field contains all species-group names that have been applied to Western Atlantic mollusks. In the case of currently used specific or subspecific names, the name is repeated here. Synonymous names, misspellings, and misidentifications are entered only here. For *nomina dubia,* the specific name is entered both here and under **species**. If a Western Atlantic species is known from other ocean basins, all known synonyms worldwide are listed.

STATUS 1: Describes the status of a given **associated name:** V = valid (i.e. currently recognized); + = synonym (including misspellings and misidentifications); X = extralimital (for names formerly attributed to the Western Atlantic fauna); D = *nomen dubium* (used to mean "not yet identified" rather than "unidentifiable"). Only one code can be entered for a given name; for synonyms of *nomina dubia,* "D" takes priority over "+."

STATUS 2: Gives additional status information about the **associated name**: ? = questionable synonymy; N = name not available for nomenclatural purposes; S = currently recognized subspecific name; O = objective synonym of the valid name; + = synonym of *nomen dubium*. More than one code can be entered, possible combinations being ?N, ?+, N+, and ?N+.

AUTHOR: The author of a name is here strictly interpreted as the person responsible for a name's being available. Authors of non-binomial, manuscript or nude names later made available are cited under **attributed author**. For misidentifications, "auct. non *x*" is entered; for misspellings, just "auct." The author responsible for the misidentification or misspelling is entered under **attributed author**. Variant spellings are treated as misspellings unless there is strong evidence that they are intentional, in which case they are treated as emendations. The **author** of a justified emendation is the original author, of an unjustified emendation the emending author. In the case of variant spellings in the original publication, the author's intended spelling is used when this is obvious, with other spellings treated as misspellings.

Constructions such as "*x* in *y*" are avoided by citing in the bibliographic database the block of text written by *x* within *y*'s work. Only in a few cases has this proved impossible, for example, Verrill and Smith in Verrill, where scattered descriptions in Verrill's work are attributed to Verrill and Smith.

DATE: The date of publication is the year in which a name was made available. The exact day and month of publication, if known, and references thereto, are given in the bibliographic database, where the stated date of publication is distinguished from the true date of publication. Misspellings and misidentifications do not have dates of publication in this sense.

ABC: This field distinguishes multiple publications by an author in a single year (e.g. Dall 1889a, 1889b). The species database links to the bibliographic database through the combination of the **author, date**, and **abc** fields.

ATTRIBUTED AUTHOR: Names are often attributed to authors other than those responsible for their publication and availability. Authors of non-binomial, manuscript and nude names later made available are listed here. Other cases include ones such as names being attributed to Lamarck, 1822 by workers unaware that the names were first introduced in Lamarck, 1816. Authors responsible for misspellings and misidentifications are also entered here, not under **author.**

ORIGINAL GENUS: The genus in which the name in **associated name** was placed when first published. Some authors, such as Dall (1889a), often used subgeneric names as if they were generic names, with the generic name placed in a heading. The original genus is taken to be the name that the author stated was the generic name, in accordance with ICZN rules.

PARENTHESES (): If **genus** matches **original genus**, "n" (no) is placed in this field, indicating that no parentheses are needed around author and date when citing the species

Figure 1. Selected fields from the database, showing species of Neritopsidae, Phenacolepadidae, and Pleurotomariidae.

Genus	Species	Subspecies	Status 1	Status 2	Associated name	Author	Date	Abc
Neritopsis	*atlantica*		V		atlantica	Sarasúa	1973	
Neritopsis	*atlantica*		+		finlayi	Hoerle	1974	
Phenacolepas	*hamillei*		V		hamillei	Fischer	1857	
Phenacolepas	*hamillei*		+		antillarum	Dall	1889	a
Phenacolepas	*rushii*		V		rushii	Dall	1889	a
Entemnotrochus	*adansonianus*	*adansonianus*	V		adansonianus	Crosse & Fischer	1861	
Entemnotrochus	*adansonianus*	*bermudensis*	V	S	bermudensis	Okutani & Goto	1983	
Perotrochus	*amabilis*		V		amabilis	Bayer	1963	
Perotrochus	*atlanticus*		V		atlanticus	Rios & Matthews	1968	
Perotrochus	*charlestonensis*		V		charlestonensis	Askew	1988	
Perotrochus	*gemma*		V		gemma	Bayer	1965	
Perotrochus	*lucaya*		V		lucaya	Bayer	1965	
Perotrochus	*maureri*		V		maureri	Harasewych & Askew	1993	
Perotrochus	*maureri*		+	N	amabilis	auct. non Bayer	1963	
Perotrochus	*midas*		V		midas	Bayer	1965	
Perotrochus	*notialis*		V		notialis	Leme & Penna	1969	
Perotrochus	*pyramus*		V		pyramus	Bayer	1967	
Perotrochus	*quoyanus*	*quoyanus*	V		quoyanus	Fischer & Bernardi	1856	
Perotrochus	*quoyanus*	*insularis*	V	S	insularis	Okutani & Goto	1985	

name. If they do not match, "y" (yes) indicates that parentheses are needed. This comparison can be automated, except in cases where the original genus was misspelled. For example, if **original genus** is *"Litorina"* and genus is *"Littorina,"* "n" is entered. Other common examples include *"Actaeon"* vs *"Acteon," "Mangilia"* vs *"Mangelia,"* and *"Homalogyra"* vs *"Omalogyra."*

COMBINING GENERA: This field lists genera (and subgenera) with which **associated name** has been combined in the literature.

COMBINATION: Citation of the original combination of names is in the format "Genus (Subgenus) {Section} species status infraspecific-names" along with any notations of uncertainty, such as a genus with a query (?). For "status" the type of name (variety, form, etc.) for infrasubspecific names is indicated. Some authors, such as Dall (1889a) have used sectional in addition to generic and subgeneric names; these are placed in curly braces {}.

CITATION: The pages on which a name is introduced. The entire page range is cited, not just the starting page, to assist interlibrary loan requests. Occurrences of names in indices or tables of contents are not cited unless alternate spellings occur there.

FIGURE: The plate and figure numbers in the original publication. These are separated from **citation** to allow them to be sorted independently, to check, for example, whether all of the figures in a given publication have been cited.

OTHER FIGURE: Illustrations of type specimens not figured in the original publication are cited here. Such illustrations may have been referred to in the original publication (indications), or have been published subsequent to it. Photographs or otherwise improved illustrations of previously figured types are also cited here.

TYPE LOCALITY: It is difficult to eliminate a subjective element in the citation of type localities. Authors frequently give only part of the locality information in the original description, with the rest being contained in the introduction of an article, or an appendix giving station numbers. Country is often omitted entirely by authors who consider it to be obvious. Citations of type localities are therefore paraphrased based on all information available in the original publication, with interpretative comments added in brackets as necessary. In many cases an author lists more than one locality, without explicitly stating a type locality, or mentioning which locality the holotype came from. If an author neglected to state a locality, "not stated" is entered; if an author did not know the locality, "unknown" is entered. Restrictions of type localities by subsequent authors are given in brackets at the end of the field.

ALL LOCALITIES: Abbreviations were assigned to numerous localities at the level of state, province, and island throughout the Western Atlantic (e.g., Lab =

Fig. 1. (continued)

( )	Original genus	North	South	West	East	Shallow	Deep	Shallow live	Deep live	Size
n	*Neritopsis*	23	-20.5	82.5	29.3	0	20			16
n	*Neritopsis*	23	23	82.8	81.3	0	0			17
y	*Acmaea*	28	-28	87	36	0	3			8
y	*Scutellina*	25	25	82	82	0	0			8
y	*Umbraculum*	26	9	80	65	55	55			10
y	*Pleurotomaria*	26.48	13.06	78.67	59.62	107	482	107	366	146
n	*Entemnotrochus*	32.3	32.3	64.8	64.8	366	366			56
y	*Mikadotrochus*	27.73	23	93	80.86	128	411	219	219	80
n	*Perotrochus*	-24	-31	51	45	133	200			72
n	*Perotrochus*	32.73	32.73	78.09	78.09	213	213			87
n	*Perotrochus*	13.2	13.2	59.6	59.6	183	183			47
n	*Perotrochus*	26.48	26.48	78.67	78.67	320	320			32
n	*Perotrochus*	32.73	30.3	80	78.09	193	366	195	213	60
n		32.73	32.73	78.1	78.1	210	198	210	198	45
n	*Perotrochus*	25.93	25.93	78.12	78.12	650	650			118
y	*Mikadotrochus*	-32	-32	51	51	150	150			74
n	*Perotrochus*	16.29	16.29	61.16	61.16	600	600			48
y	*Pleurotomaria*	21.79	12.55	86.4	59.65	128	549	134	350	57
n	*Perotrochus*	32.3	32.3	64.8	64.8	366	366			54

Labrador; Ber = Bermuda; FVen = Falcón, Venezuela). These allow species distributions to be documented more precisely than by **north, south, east**, and **west** described below. Abbreviations are summarized in a separate database table.

OCEAN: Distributions of Western Atlantic species in other oceanic regions are tracked with the following abbreviations: WA = Western Atlantic, EA = Eastern Atlantic, IO = Indian Ocean, WP = Western Pacific, EP = Eastern Pacific, AO = Arctic Ocean, SO = Southern Ocean. Data in **north, south**, and the four **depth** fields are taken only from Western Atlantic records.

SHELL: Four abbreviations (s = shell, i = internal shell, v = vestigial shell, n = no shell) can be used, for example to look at the systematic distribution of shell reduction and loss, or to include only readily fossilizable taxa in comparisons to the fossil record.

NORTH: The farthest north in decimal degrees that the **associated name** has been reported in the Western Atlantic, from the mid-Atlantic ridge westward, including East Greenland, but excluding Iceland.

Latitudes and longitudes are converted to decimal degrees, allowing this and the next three fields to be numeric rather than alphanumeric. Database programs allow mathematical operations on numeric fields but not on alphanumeric ones. Latitudes below the equator are entered as negative numbers, e.g. 23°25'S is entered as -23.42.

SOUTH: The farthest south in decimal degrees that the **associated name** has been reported in the Western Atlantic, including the Antarctic Peninsula, Tierra del Fuego, and Ascension Island, but not St. Helena.

EAST: The farthest east in decimal degrees that the **associated name** has been reported in the Atlantic, limited to a minimum of zero. Longitudes east of Greenwich are not reported.

WEST: The farthest west in decimal degrees that the **associated name** has been reported, to a maximum of 180° for circumtropical or circumpolar species. Longitudes west of 180° are not reported.

SHALLOW: The shallowest depth in meters, with "0" indicating intertidal or beach-collected specimens. Note: in this and the other three depth fields, only "proven" depths are reported. If a species has been reported only in one dredge haul from 100-130 meters, "130" is entered in **shallow** and "100" in **deep**, corresponding to the shallowest and deepest it has been proven to occur. Similarly, if it is known from two dredge hauls, one from 100-130 meters, the other from 170-190, "130" is entered in **shallow** and "170" in **deep**.

DEEP: The deepest recorded depth in meters. Exact conversions are given from feet and fathoms, with the caveat that this can imply accuracy not inherent in the original number (e.g. 100 fathoms = 183 meters).

LIVE SHALLOW: The shallowest depth in meters reported for live-collected specimens, with negative numbers indicating supratidal occurrence.

LIVE DEEP: The deepest depth in meters reported for live-collected specimens.

SIZE: The maximum size, in millimeters, for any dimension.

COMMENTS: Any comments necessary to explain or modify entries in other fields. Preoccupied, replacement, nude, and non-binomial names are noted here. If an author declared a name to be a *nomen oblitum* during the period when that provision of the ICZN was in force, that is noted here.

REFERENCES: Sources of information in the other fields are documented here by citation of author and date followed by a series of codes: D = maximum depth; d = minimum depth; L = maximum live depth; l = minimum live depth; N = north; S = south; E = east; W = west; M = maximum size; C = current classification; + = synonymy; V = valid; T = lectotype or neotype designation or restriction of type locality. Multiple references are separated by semicolons. A typical entry in **references** might look like this: Dall (1889a) DLlW; Abbott (1974) dNM; Leal (1991) SE.

Other fields beyond those noted here are possible, and can be added depending on the needs of a particular researcher. One could record protoconch size and whorl number; references to protoconch, radular and anatomical illustrations; substrate preference; feeding type; reproductive mode; depositories and catalogue numbers of type specimens; and so on, *ad infinitum.*

RESULTS AND DISCUSSION

WESTERN ATLANTIC GASTROPOD DIVERSITY

The database currently contains 8370 records for Western Atlantic marine gastropods from Greenland and Northern Canada through Antarctica. Statistics concerning these records are summarized in Table 2. Of these records, 3988 are for species currently recognized as valid. This means that the species has not been synonymized since it was named, or if it has been synonymized, some author has presented strong arguments that it should be taken out of synonymy.

Currently recognized species somewhat outnumber the 3491 validly published synonyms. The synonymy ratio is 0.88:1, about half the 1.64:1 estimated by Clench (1959) for the Western Atlantic. Boss (1971) has estimated synonymy ratios for mollusks overall to be in the range of 4:1. This ratio would predict 1496 valid species and 5983 synonyms among the 7479 names for Western Atlantic gastropods, and is clearly far too high for Western Atlantic gastropods. This may reflect that most Western Atlantic workers have introduced names for full species; the tradition of naming varieties and forms is not as strong as it has been historically among European workers. Undoubtedly many species listed as valid will be synonymized once monographic work on particular families is done, but other species will be taken out of synonymy, and new species will continue to be discovered. Synonymy ratios for Western Atlantic gastropods are unlikely to significantly exceed 1:1.

Table 2. Composition of records in the Western Atlantic marine gastropod database.

CURRENTLY RECOGNIZED SPECIES		3988
Tropical	3103	
Caribbean	2164	
Northern	413	
Southern	472	
NOMINA DUBIA		157
SYNONYMS		4189
validly published	3491	
invalidly published	78	
misidentifications	435	
misspellings	185	
EXTRALIMITAL		36*
TOTAL RECORDS		8370

*includes one land snail erroneously described as marine.

Of the 3988 currently recognized species, 3103 (78%) occur in tropical or semitropical areas, here defined as extending from Cape Hatteras to Rio de Janeiro, Brazil (south of 35°N to north of 24°S). Of these, 2164 occur in, but are not necessarily restricted to, the Caribbean region (south of 24°N, north of 8°N; west of 59°W, east of 88°W). About 413 species are restricted primarily to northern areas (north of 35°N) and 472 to southern areas (south of 24°S).

The only estimate of the size of the entire Western Atlantic molluscan fauna appears to be that of Clench (1959), who predicted (without documentation) that it "would exceed 6,000 species and subspecies, but would not reach 8,000 species and subspecies." Abbott (1974) lists 4491 species of marine gastropods in the Americas (Western Atlantic and Eastern Pacific) and 1918 species in other classes, giving a ratio of 2.34 gastropods species per non-gastropod. The total of 3988 marine gastropods in the

database therefore implies that there should be about 1700 non-gastropod mollusks in the Western Atlantic. Thus, known diversity of Western Atlantic mollusks is about 5700 species, substantiating Clench's prediction that total diversity will exceed 6,000 species as knowledge of the fauna increases.

The estimate of 3100 species of gastropods in the tropical Western Atlantic is considerably higher than previously thought. The tropical Western Atlantic molluscan fauna is usually considered less diverse than that of the tropical Eastern Pacific. Keen (1971:2) stated "at the moment, preliminary lists suggest that the Pacific side, in spite of its narrow continental shelf, has more species." However, Keen lists only 2438 species of gastropods named by 1971 in the tropical Eastern Pacific. Of the 3103 Western Atlantic species, 2641 had been named by 1971. Given the uncertainty in these numbers, the diversity levels of these faunas must be considered indistinguishable.

Although there has never been a reliable estimate of the diversity of Western Atlantic gastropods, a number of authors have discussed the impoverishment of the fauna as compared to the Eastern Pacific (Olsson, 1961; Woodring, 1966; Vermeij, 1978, 1991; Stanley and Campbell, 1981; Stanley, 1986). Olsson (1961:2) stated, "As compared to its richness in the Miocene, the present-day Caribbean mollusks appear strangely modified and greatly impoverished; on the other hand, the Panamic-Pacific molluscan fauna has remained fundamentally unchanged." Stanley and Campbell (1981) demonstrated that Pliocene faunas in the Western Atlantic were 70-80% extinct, whereas Pliocene faunas of California were only 30% extinct. They invoked the higher extinction rates in the Western Atlantic to explain the depauperate Recent fauna in the region.

As demonstrated here, the gastropod fauna of the tropical Western Atlantic is not depauperate compared to that of the tropical Eastern Pacific. Previous workers have been attempting to explain a myth. It is true that the Western Atlantic fauna has undergone substantial extinction, but it is not possible to demonstrate that this has led to an overall decline in diversity. Other processes, such as speciation and immigration must be balancing extinction (Allmon *et al.*, 1993). It is possible that the Western Atlantic fauna is depauperate in shallow water as compared to that of the Eastern Pacific, with greater diversity in deeper water, where there is considerably more continental shelf area than in the Eastern Pacific. This possibility would be easily testable if data on Eastern Pacific mollusks were available in database form.

WESTERN ATLANTIC GASTROPOD BIOGEOGRAPHY

Comparisons of the faunas in different parts of the Western Atlantic have been complicated by the different names and combinations in use for a given species. Different emphases in regional sampling cause further problems. In one area workers have concentrated on micromollusks, in another the deep water fauna is virtually unknown. The database approach allows standardization of faunal lists by cross-referencing synonyms and generic placements. Collecting biases can be accounted for by excluding particular size, depth, or taxonomic ranges.

Eight selected regions of the tropical Western Atlantic serve to demonstrate the value of databases for making faunal comparisons. These are eastern and western Florida, Yucatan, Panama, Jamaica, Puerto Rico, the Netherlands Antilles and northern Brazil. Table 3 summarizes the total number of shelled gastropod species in these faunas. Shell-less species have been excluded from the comparisons because of great variability in regional reporting: more than 10% of the Brazilian fauna falls in the shell-less category, but only 3% of the reported Panamanian fauna. Table 3 also gives totals adjusted for depth (species occurring in less than 50 meters) and size (species with maximum size greater than 5 mm). Table 4 shows for each

Table 3. Number of marine gastropod species in selected tropical Western Atlantic faunas, with restrictions by size and bathymetry to standarize faunal comparisons.

Region	Total shelled	depth <50m		size >5mm		<50m + >5mm	
		#	%	#	%	#	%
Western Florida	709	590	.83	577	.81	468	.66
Eastern Florida	778	663	.85	623	.80	529	.68
Yucatan	594	528	.89	490	.82	431	.73
Panama	444	423	.95	353	.80	332	.75
Jamaica	443	432	.98	381	.86	370	.84
Puerto Rico	674	546	.81	542	.80	450	.67
Neth. Antilles	678	662	.98	491	.72	480	.71
Northern Brazil	709	593	.84	589	.83	492	.69

Table 4. Percentage of species in common among the tropical Western Atlantic faunas in Table 3. The percentage reflects the proportion of species in the smaller fauna not reported in the larger fauna. Numbers are calculated based on the species greater than 5 mm occurring in less than 50 meters (column 7 of Table 3). Numbers below and above the diagonal are identical; both sets are included for ease of use.

REGION	WFL	EFL	Yuc	Pan	Jam	PR	NA	NBr
Western Florida	–	.75	.66	.50	.51	.54	.47	.56
Eastern Florida	.75	–	.71	.64	.66	.67	.58	.62
Yucatan	.66	.71	–	.67	.69	.67	.63	.56
Panama	.50	.64	.67	–	.65	.72	.72	.60
Jamaica	.51	.66	.69	.65	–	.79	.77	.61
Puerto Rico	.54	.67	.67	.72	.79	–	.74	.67
Neth. Antilles	.47	.58	.63	.72	.77	.74	–	.59
Northern Brazil	.56	.62	.56	.60	.61	.67	.59	–

pair of faunas the percentage of species that the smaller fauna has in common with the larger one. This is the Simpson Index (Simpson, 1943), which is appropriate for large faunal lists corrected for sampling biases (Alroy 1992). Important sources of information and results concerning faunal composition for each of these areas are discussed below.

Western and Eastern Florida: Faunal lists for western and eastern Florida north of 25°N (i.e. excluding the Florida Keys) were compiled from Lyons (1989) and all papers on mollusks of Florida cited in the bibliography therein, Springer and Bullis (1956), Perry and Schwengel (1955), Maury (1922), and all papers on mollusks of Florida published in *Nautilus* in the last 70 years. Records from Dall (1927) are excluded because the Fernandina, Florida station is actually off Georgia. Uncertain records were checked by reference to the collections at ANSP.

Three-quarters of all species from western Florida are also known from eastern Florida. Diversity is higher in eastern Florida than western Florida, probably because of a greater diversity of habitats in the former. Eastern Florida has more reefal, hard substrate areas than western Florida, which has mainly soft bottom. Reefal habitats in western Florida are restricted to patchy areas off-shore, such as the Florida Middle Grounds (Lyons, 1976; Turgeon and Lyons, 1977; Hopkins *et al.*, 1977). Five of the seven faunal regions have lowest similarity with western Florida, reflecting the absence of shallow reefal habitat there that is available in the other areas. Western Florida is most similar to eastern Florida and Yucatan, the two areas closest to it geographically.

Yucatan: The faunal list for Yucatan (the entire Yucatan Peninsula) is derived mainly from Vokes and Vokes (1983). Additional records, mostly for deep water mollusks, come from Dall (1881, 1889a). Yucatan shows greater faunal similarity to eastern Florida (71%) than to western Florida (66%), although it is geographically closer to western Florida. Yucatan shares with eastern Florida a strong shallow-water reefal faunal component that is absent in western Florida.

Panama: The faunal list for Panama comes mainly from Olsson and McGinty (1958) and Radwin (1969). The few available records deeper than 50 meters come from Petuch (1990).

Jamaica: Records from Jamaica come primarily from Humfrey (1975), but species that he listed under "Other Jamaican Gastropods" on pages 198-205 were excluded unless confirmed by other sources. All of C.B. Adams' Jamaican marine gastropods as documented by Clench and Turner (1950) are included, synonymized as appropriate.

Puerto Rico: Puerto Rican records are taken mainly from Warmke and Abbott (1961), Ortiz-Corps (1983) and Dall and Simpson (1901). Many deep water records come from Watson (1886). Puerto Rico shows greatest faunal similarity to Jamaica (79%) and the Netherlands Antilles (74%), the two closest points among the regions compared here.

Puerto Rico and the Netherlands Antilles are about equidistant from northern Brazil but the Brazilian fauna is more similar to that of Puerto Rico (67%) than to that of the Netherlands Antilles (59%). Puerto Rico and the Netherlands Antilles share 74% of their species. Puerto Rico shares 62 species with northern Brazil that it does not share with the Netherlands Antilles. There is no obvious pattern in taxonomy or habitat preference among these species, but it is possible that they tend to be deeper water species. The average minimum depth for species occurring in less than 50 meters depth is between 3 and 4 meters in both Puerto Rico and the Netherlands Antilles. The species shared by Puerto Rico and Brazil but not the Netherlands Antilles have an average minimum depth of 9.5 meters. Collecting in moderate depths (10 to 50 meters) in the Netherlands Antilles should increase the apparent similarity with the Brazilian fauna.

Netherlands Antilles: The primary source of information is Jong and Coomans (1988). Virtually no information is available about deep-water mollusks of this region; only 3% of the gastropods known from the area are restricted to depths below 50 meters. On the other hand, the micromolluscan fauna is extremely well known because of the work of Jong and Coomans and their colleagues. About one quarter of the gastropod species reported from the Netherlands Antilles do not exceed 5 mm at maturity, a higher percentage than reported anywhere else in the Western Atlantic.

Northern Brazil: Because of the enormous extent of the Brazilian coastline, comparisons were restricted to northern Brazil. Only those species whose geographic ranges lie within or cross the zone from 4°N to 6°S (Amapá to Rio Grande do Norte) were included. The two primary sources are Rios (1985) and Leal (1991). Rios (1975) gave more precise station data than in 1985; Rios (1970) provided maps showing the locations of many stations. Leal (1991) documented the faunas of Atol das Rocas and Fernando de Noronha, which are included in this zone.

The average similarity of the Brazilian fauna to other tropical Western Atlantic faunas is 0.60, somewhat lower than the average similarities for the other areas, which range from 0.64 to 0.69 (except western Florida at 0.57).

This is consistent with its geographical remoteness from the Caribbean area.

Western Atlantic: Of 28 pairwise comparisons between eight Western Atlantic faunas, only a single one yields a similarity lower than 50%: that between western Florida and the Netherlands Antilles. All other values are above 50%, as expected for regions within a single biogeographic province. Of the 3103 gastropod species occurring in the tropical Western Atlantic province, 2497 (80%) are restricted to that region. Coomans (1962) defines a biogeographic province (which he calls an "autonomous zoogeographical province") as having at least 50% endemic species.

There seems to be little basis for recognizing biogeographic subprovinces within the tropical Western Atlantic, because similarities between regional faunas are determined as much by habitat availability as by geographic proximity. As shown in Table 5, no local region of the Western Atlantic has more than about 4% endemics, excluding species named since 1980 as these are likely to be discovered in other areas once attention has been called to their existence. Such low levels of endemicity are insufficient to make faunal province subdivisions. Coomans (1962) lumped the Virginian area (Cape Hatteras to Cape Cod) into the Boreal Province because it had only 10.5% endemic species.

Tropical Western Atlantic endemics are not concentrated in one area, although they appear more common on continental margins than on islands. Petuch (1990) named the Blasian faunal subregion for the Caribbean coast of Panama and Costa Rica, but Panama (including Costa Rica) has only about 4% endemic species (Table 5). Jong and Coomans (1988) named a number of species from the Netherlands Antilles increasing apparent endemicity, but many of these have been identified in samples from the Bahamas at ANSP (J. Worsfold, pers. comm.). Thus, even as our knowledge of regional Western Atlantic faunas increases, it is unlikely that the percentage of narrow ranging endemics will increase. Diversity in the tropical Western Atlantic is, however, higher than has been commonly perceived, and many local faunas have been badly under-sampled.

Table 5. Number and percentage of endemic species in the faunas in Table 3. The second column repeats the totals from the seventh column of that table.

Region	<50m, >5mm	Endemic #	%
Western Florida	468	17	3.6
Eastern Florida	529	9	1.7
Yucatan	431	10	2.3
Panama	332	14	4.2
Jamaica	370	2	0.5
Puerto Rico	450	4	0.9
Neth. Antilles	480	14	2.9
Northern Brazil	492	14	2.8

In 1901, Dall and Simpson estimated "the average American marine tropical shell-fauna" to contain about 600 species. Five of the eight faunas discussed here exceed 600 species of gastropods alone. A hint of the diversity yet to be discovered comes from the Worsfold collection at ANSP, which documents about 1550 species of Bahamian mollusks. Because most species in the tropical Western Atlantic are widespread, as indicated by the high similarities of the eight widely separated faunas studied here, diversity in the Bahamas should be considered typical of the faunal province as a whole. Most local faunas in the tropical Western Atlantic will eventually be demonstrated to have in excess of 1500 species of Recent marine mollusks.

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